

VISION RESEARCH

Founded by THORNE SHIPLEY

Chairman and Editor-in-Chief

David H. Foster, Schools of Electrical & Electronic Engineering and Life Sciences, University of Manchester, Manchester M13 9PL, U.K.

Vision Research Editorial Office

Vision Research Editorial Office, c/o Elsevier, 525 B Street, San Diego, CA 92101-4495, U.S.A. E-mail: VR@elsevier.com

Vision Research is a journal devoted to the functional aspects of human, vertebrate and invertebrate vision and welcomes papers that address important issues in basic and/or clinical research.

Senior Editors

WOLFGANG BAEHR, Salt Lake City, UT, U.S.A.
FRED KINGDOM, Montreal, Canada
RICHARD KRAUZLIS, La Jolla, CA, U.S.A.
MICHAEL S. LANDY, New York, NY, U.S.A.
FRANK SCHAEFFEL, Tübingen, Germany

The Senior Editors are assisted by an Editorial Board consisting of:

DAVID ALAIS, Sydney, Australia
JOCHEN BRAUN, Magdeburg, Germany
FRANK BREMMER, Marburg, Germany
ELI M. BRENNER, Amsterdam, The Netherlands
STEPHEN A. BURNS, Bloomington, IN, U.S.A.
SUSANA CHUNG, Berkeley, CA, U.S.A.
KARL R. GEGENFURTNER, Giessen, Germany
JULIE HARRIS, St. Andrews, Fife, U.K.
LYNNE KIROPES, New York, NY, U.S.A.
PAUL R. MARTIN, Carlton, Vic., Australia
PAUL V. MCGRAW, Nottingham, U.K.
SHIN'YA NISHIDA, Atsugi, Kanagawa, Japan
ANTHONY NORCIA, Stanford, CA, U.S.A.
BRUNO OLSHAUSEN, Berkeley, CA, U.S.A.
LYNN OLZAK, Oxford, OH, U.S.A.
MICHAEL PARADISO, Providence, RI, U.S.A.
SCOTT STEVENSON, Houston, TX, U.S.A.
ANDREW STOCKMAN, London, U.K.
SIMON THORPE, Toulouse, France
DAVID TROILO, New York, NY, U.S.A.
PREETI VERGHESE, San Francisco, CA, U.S.A.
JOHNATHAN VICTOR, New York, NY, U.S.A.
MIKE A. WEBSTER, Reno, NV, U.S.A.
DAVID WHITNEY, Berkeley, CA, U.S.A.
FELIX WICHMANN, Tübingen, Germany
CONG YU, Beijing, China

Publication information: *Vision Research* (ISSN 0042-6989) is published monthly by Elsevier (Radarweg 29, 1043 NX Amsterdam, The Netherlands) and distributed by Elsevier, 360 Park Avenue South, New York, NY 10010-1710, USA. Periodicals Postage Paid at New York, NY and at additional mailing offices (not valid for journal supplements). USA POSTMASTER: Send change of address to *Vision Research*, Elsevier Customer Service Department, 3251 Riverport Lane, Maryland Heights, MO 63043, USA.

Orders, claims, and journal inquiries: Please contact the Elsevier Customer Service Department nearest you: **St. Louis:** Elsevier Customer Service Department, 3251 Riverport Lane, Maryland Heights, MO 63043, USA; phone: (877) 8397126 [toll free within the USA]; (+1) (314) 4478878 [outside the USA]; fax: (+1) (314) 4478077; e-mail: JournalCustomerService-usa@elsevier.com. **Oxford:** Elsevier Customer Service Department, The Boulevard, Langford Lane, Kidlington, Oxford OX5 1GB, UK; phone: (+44) (1865) 843434; fax: (+44) (1865) 843970; e-mail: JournalsCustomerServiceEMEA@elsevier.com. **Tokyo:** Elsevier Customer Service Department, 4F Higashi-Azabu, 1-Chome Bldg, 1-9-15 Higashi-Azabu, Minato-ku, Tokyo 106-0044, Japan; phone: (+81) (3) 5561 5037; fax: (+81) (3) 5561 5047; e-mail: JournalsCustomerServiceJapan@elsevier.com. **Singapore:** Elsevier Customer Service Department, 3 Killiney Road, #08-01 Winsland House I, Singapore 239519; phone: (+65) 63490222; fax: (+65) 67331510; e-mail: JournalsCustomerServiceAPAC@elsevier.com.

Author inquiries: You can track your submitted article at http://help.elsevier.com/app/answers/detail/a_id/89/p/8045/. You can track your accepted article at <http://www.elsevier.com/trackarticle>. You are also welcome to contact Customer Support via <http://support.elsevier.com>.


Language (usage and editing services): Please write your text in good English (American or British usage is accepted, but not a mixture of these). Authors who feel their English language manuscript may require editing to eliminate possible grammatical or spelling errors and to conform to correct scientific English may wish to use the English Language Editing service available from Elsevier's WebShop <http://webshop.elsevier.com/languageediting/> or visit our customer support site <http://support.elsevier.com> for more information.

Illustration services: Elsevier's WebShop (<http://webshop.elsevier.com/illustrationservices>) offers Illustration Services to authors preparing to submit a manuscript but concerned about the quality of the images accompanying their article. Elsevier's expert illustrators can produce scientific, technical and medical-style images, as well as a full range of charts, tables and graphs. Image 'polishing' is also available, where our illustrators take your image(s) and improve them to a professional standard. Please visit the website to find out more.

Advertising information: If you are interested in advertising or other commercial opportunities please e-mail Commercialsales@elsevier.com and your inquiry will be passed to the correct person who will respond to you within 48 hours.

Funding body agreements and policies: Elsevier has established agreements and developed policies to allow authors whose articles appear in journals published by Elsevier, to comply with potential manuscript archiving requirements as specified as conditions of their grant awards. To learn more about existing agreements and policies please visit <http://www.elsevier.com/fundingbodies>.

Printed by Sheridan Digital Express in the United States of America

 The paper used in this publication meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper)

Front cover illustration: see p. 38.